PRE- TO POST-FLEDGING CARRYOVER EFFECTS AND THE POST-FLEDGING ECOLOGY OF THE DICKCISSEL (*SPIZA AMERICANA*)

BY

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THESIS

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ABSTRACT

The post-fledging period—defined as the time between when a bird leaves its nest and disperses or migrates—is a critical stage in the avian life cycle. Past research has identified survival during this stage as a key component in population growth and maintenance of avian species. Therefore, understanding causes of variation in fledgling survival may be of critical importance in conserving avian biodiversity. I examined the post-fledging ecology of the Dickcissel (*Spiza americana*), with emphasis on pre- to post-fledging carryover effects of nestling traits and fledgling habitat use. Specifically, I sought to address the following questions: (1) Do body condition and wing development at fledging predict juvenile survival during the post-fledging period? (2) What is the relative influence of body condition and wing development on cause-specific mortality (predation and exposure) of fledglings? (3)What is the relative influence of body condition and wing development on cause-specific mortality of fledglings compared to other potential factors? (4) What post-fledging micro-habitat characteristics do fledglings prefer to use? (5) Are habitat characteristics selected by fledglings the same as those selected for nesting by breeding adults? (6) Do habitat characteristics selected by fledglings benefit fledgling survival? From May to August of 2014 and 2015, I radio-tagged, quantified body condition and wing development at fledging, and monitored the survival of 104 fledgling Dickcissels in two grasslands of central Illinois, USA. For fledglings that died, I attempted to identify the cause of death: either death due to predation or death due to exposure. While documenting fledgling survival, I also quantified vegetation characteristics at 323 fledgling locations, 323 random locations, and 52 nest locations of 60 different fledglings. Additionally, I

used automated radio telemetry systems (ARTS) to document fledgling activity rates continuously during the post-fledging period.

I found pre- to post-fledging carryover effects of body condition and wing development at fledging, in which traits were positively associated with survival during the early part of the post-fledging period. Survival benefits of each trait depended on cause-specific sources of mortality, such that individuals in better body condition were less likely to die from exposure while those with more advance wing development were less likely to be preyed upon. Fledglings in better condition and with more advance wing development were comparatively more active and mobile earlier in the post-fledging period, suggesting they were better able to evade and/or hide from predators. Fledglings preferred areas with greater vegetation density (higher, denser, and more concealed) which were positively correlated with post-fledging survival. Preferred habitat of fledglings did not differ from nesting habitat. Collectively, my results add to a growing literature on the post-fledging ecology of birds, document several ways by which young songbirds mitigate the high risks of mortality during the early post-fledging period, and highlight important considerations for wildlife programs designed to conserve avian biodiversity.

To my parents (Eric and Sheryl) whose influence exposed me to the natural sciences and drove me to become the scientist I am today, and to my wife Emilie who loves and supports me in all my endeavors.

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PREFACE: Thesis Format

In chapter 1, I present a literature review of the post-fledging ecology of birds with emphasis on fledgling survival and habitat use. Chapters 2 and 3 use the Dickcissel (*Spiza americana*) as a focal species to examine their respective topics. In chapter 2, I examine pre- to post-fledging carryover effects of nestling body condition and wing development on fledgling survival and cause-specific mortality. I also examine how such effects compare with other potential factors influencing fledgling survival, and associations with underlying mechanisms of survival such as activity rates. In chapter 3, I explore and compare habitat use between fledgling and random locations, and fledgling and nest locations. Furthermore, I examine associations amongst preferred habitat characteristics of fledglings and post-fledging survival.

CHAPTER 1: Post-fledging Ecology of Birds: A Literature Review

1.1 Background

The post-fledging period of birds—the time between when a bird leaves its nest and when it migrates or disperses, is a critical life history stage for birds (Cox et al. 2014). Once limited by technology, the study of post-fledging ecology has grown rapidly with the development of smaller, lighter, and longer lasting transmitters that can now be deployed on birds ranging from large eagles (Buehler et al. 1995) to hummingbirds (Hadly and Betts 2009). Given the importance of post-fledging juvenile survival in bird population growth and stability (Anders et al. 1997, Anders and Marshall 2005), and growing concerns over population declines and avian conservation worldwide (NABCI 2014), most post-fledging studies have focused on fledgling survival, and to a lesser extent habitat and space use of fledglings.

Prior to advancements in radio technology, post-fledging survival was often measured via methods that are inherently flawed and would often over or underestimate true rates of survivorship (e.g. Ricklefs 1973, Greenberg 1980, Temple and Crary 1988). Today, however, radio-telemetry has provided more robust and accurate measures of post-fledging survival in many species. Although studies of fledgling survival are often specific to a species, habitat, and/or region (Cox et al. 2014), studies have documented several consistent. Post-fledging mortality tends to be highest (up to 80%; Rush and Stutchbury 2008) during the first 5-7 days post-fledging, with survival improving with age (e.g. Sullivan 1989, Naef-Daenzer 2001, King et al. 2006, Yackel Adams 2006, Berkeley et al. 2007, Vitz and Rodewald 2011). This trend is often attributed to changes in fledgling development, as fledglings leave the nest at early stages of development, relatively immobile, and therefore more vulnerable to mortality (Anders 1997,

Vega Rivera 1998). As fledglings age, however, they grow and acquire characteristics that make them more adult like and less susceptible to mortality. Besides the first 0-7 days post-fledging, high rates of mortality also tend to occur when fledglings become independent from adults and begin moving farther from their natal sites (Sullivan 1989, Anders et al. 1997, Davies and Restani 2006, Wiens et al. 2006). Documentation of post-fledging survival in tropical species is rare, but findings suggest that survival rates are higher for tropical species as compared to their temperate counterparts (Tarwater and Brawn 2010).

Predation is the primary source of mortality in fledgling birds (Sullivan 1989, Anders et al. 1997, Schmidt et al. 2008, Ausprey and Rodewald 2011, Balogh et al. 2011). Although identifying predators is difficult, direct observations and anecdotal evidence point to a wide range of species. Raptors and snakes are the most common culprits (e.g. Anders 1997, Kershner et al. 2004, King et al. 2006, Suedkamp Wells et al. 2007, Ausprey and Rodewald 2011, Vitz and Rodewald 2011), but other species such as small rodents (e.g. chipmunks and squirrels; Anders 1997, Davies and Restani 2006, King et al. 2006, Schmidt et al. 2008, Balogh et al. 2011), martens (Naef-Daenzer et al. 2001), raccoons (*Procyon lotor*; Schmidt et al. 2008), badgers (*Taxidea taxus*; Davies and Restani 2006), domestics cats (*Felis catus*; Balogh et al. 2011, Ausprey and Rodewald 2011, Vitz and Rodewald 2011), and non-raptor bird species such as corvids and woodpeckers (Naef-Daenzer et al. 2001) have also been documented.

Though results are largely equivocal, a wide host of physical, physiological, reproductive, environmental, and behavioral factors have been associated with fledgling survival. These include, but are not limited to body mass and body condition (Magrath 1991, Anders et al. 1997, Ausprey and Rodewald 2011, Naef-Daenzer et al. 2001, Vitz and Rodewald 2011, Maness and Anderson 2013), wing length (Morrison 2009), presence-absence of disease (Knutie et al.

2013, Krams et al. 2013), parental care (Wheelwright et al. 2003, Dybala et al. 2013), environmental conditions (Yackel Adams et al. 2006, Ausprey and Rodewald 2011, Hovick et al. 2011), clutch size (Strysky et al. 2015), and fledging or hatching date (Naef-Daenzer et al. 2001, Middleton and Green 2008). Of these factors, juvenile weight or body condition at fledging is commonly examined, with individuals that are heavier or in better condition often having greater survival prospects (e.g. Naef-Daenzer et al. 2001, Vitz and Rodewald 2011). Greater mass or better body condition is thought to buffer fledglings from the elements and provide energy reserves for avoiding predation (e.g. Magrath 1991, Anders et al. 1997, Maness and Anderson 2013). Though rarely examined, juvenile wing length or development is becoming an exciting and compelling line of research with implications for post-fledging survival (e.g. Morrison 2009) and avian life history evolution (Martin 2015). More developed wings may provide a more efficient means of avoiding, hiding from, or evading predators, which in turn should improve fledgling survival prospects (Dial et al. 2006, Morrison et al. 2009).

The other major branch of post-fledging study revolves around habitat selection, movement and dispersal, and spatial ecology of fledglings. Past research suggests that fledgling birds improve their chances of survival by selecting denser, taller, more concealed, and more complex areas of vegetation, presumably because it provides them better cover from potential predators (e.g. King et al. 2006, Berkeley et al. 2007, Rivera et al. 1998, Vitz and Rodewald 2011, Small et al. 2015). This line of evidence is encouraging as it suggests management agencies may aid fledgling survival by providing similar types of areas on their lands (Cox et al. 2014).

Fledgling movements and home ranges generally increase with age and vary by species (Anders et al. 1998, Vega Rivera et al. 1998, Kershner et al. 2004, White and Faaborg 2008, Vitz

and Rodewald 2010, Frye and Jageman 2012, Anthony et al. 2013, Streby and Anderson 2013). Movements of fledglings are thought to only occur during the day, however, some warblers in Europe appear to perform long nocturnal flights just prior to migration; the reason for which remains unclear (Bulyuk et al. 2009, Bulyuk and Mukhin 2010). Factors implicated in influencing fledgling movement and home range size include distribution of food resources and areas of cover (Anders et al. 1998, Vega Rivera et al. 1998, White and Faaborg 2008 Vitz and Rodewald 2010) and parental prey selection during the nestling period (Arnold et al. 2007).

1.2 Objectives

My research examined pre- to post-fledging carryover effects of nestling body condition and wing development on post-fledging survival and cause-specific mortality. Additionally, I compared and contrasted micro-habitat selection of fledglings to that of nest locations and areas used by breeding adults. The focal species for my research was the Dickcissel, a grassland bird experiencing significant declines since 1966 but breeding in abundance in central Illinois (Sauer et al. 2011). Specifically, I addressed the following questions and hypotheses in my thesis:

1.) *Do body condition and wing development at fledging predict juvenile survival during the post-fledging period?*

Hypothesis:

If body condition and wing development at fledging provide post-fledging survival benefits, then body condition and wing development should be positively associated with post-fledging probabilities of survival.

2.) *What is the relative influence of body condition and wing development on cause-specific mortality (predation and exposure) of fledglings?*

Hypothesis:

If body condition and wing development at fledging provide different post-fledging survival benefits against cause-specific sources of mortality, then body condition and wing development should differ in their relative influence on each source of fledgling mortality.

3.) *What is the relative influence of body condition and wing development on cause-specific mortality of fledglings compared to other potential factors?*

Hypothesis:

If body condition and wing development provide survival benefits against predation, the primary source of post-fledging mortality, then body condition and wing development should be more influential on fledgling probabilities of survival than other potential factors.

4.) *What post-fledging habitat characteristics do fledglings prefer to use?*

Hypothesis:

If denser, taller, vegetation that provides more concealed areas benefit fledgling survival, then habitat used by fledglings should be denser, taller, and provide more concealment than random areas.

5.) *Are habitat characteristics selected by fledglings the same as those selected for nesting by breeding adults?*

Hypothesis:

If denser, taller, vegetation that provides more concealed areas benefit fledgling and nest survival, then habitat used by fledglings should be the same as habitat at nest locations.

6.) *Do habitat characteristics selected by fledglings benefit fledgling survival?*

Hypothesis:

If denser, taller, vegetation that provides more concealed areas benefit fledgling survival, then fledglings using such vegetation should have better survival prospects than their counterparts.

1.3 Significance

The post-fledging period is a critical life history stage for birds, with fledgling survival rates greatly influencing species population growth and stability. Understanding factors that influence fledgling survival rates during the post-fledging period may therefore be critical to conserve the biodiversity of avian species. Because my research examines fledgling habitat use and important factors affecting fledgling survival, results should aid conservation efforts by providing information to assist management agencies in providing high-quality habitat for juvenile and breeding birds. Additionally, my findings should provide helpful insights into nestling growth strategies and improve our understanding of the evolution of life history strategies in birds.

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CHAPTER 2: Variation in Body Condition and Wing Development at Fledging Predict Post-fledging, Cause-specific Mortality in a Neotropical Migratory Songbird

2.1 Abstract

Phenotypic traits acquired in one life history stage can carryover and affect survival in subsequent stages. For songbirds, carryover effects from the pre- to post-fledging period may be crucial for survival but are poorly understood. I assessed whether juvenile body condition and wing development at fledging influence survival during the post-fledging period in the Dickcissel (*Spiza americana*). I found pre- to post-fledging carryover effects of body condition and wing development at fledging, in which traits were positively associated with survival during the early part of the post-fledging period. Survival benefits of each trait depended on cause-specific sources of mortality; individuals in better body condition were less likely to die from exposure, whereas those with more advanced wing development were less likely to be preyed upon. Fledglings with more advanced wing development were comparatively more active and mobile earlier in the post-fledging period, suggesting they were better able to evade or hide from predators. My findings document several ways in which development of phenotypic traits may aid young songbirds in mitigating high risks of mortality during the early post-fledging period. Furthermore, my results add to a growing body of evidence that factors constraining and favoring developmental processes in nestling songbirds are a fundamental aspect of avian life history strategies.

2.2 Introduction

In animals, natal dispersal is a critical life stage associated with high rates of mortality. Examples include dispersal of hatchling tortoises (Smith et al. 2013), the juvenile growth period of guppies (Arendt and Reznick 2005), and juvenile crabs seeking new shelter habitats (Beck 1995). Given that juveniles are often in early stages of development and more susceptible to various sources of mortality during such periods, variation in phenotypic traits affecting their survival may be subject to intense selection (Clutton-Brock 1988). Phenotypes developed prior to natal dispersal may therefore have important "carryover effects"—whereby conditions experienced during one biological period influence fitness of individuals during subsequent period(s) (Blomberg et al. 2014)—on juvenile survival. Thus, by determining how variation in juvenile phenotypic traits confer survival advantages, we can enhance our understanding of how traits developed in one life stage impact survival in subsequent life history stages.

For songbirds, mortality rates are notably high during the first few days of the post-fledging period—the time between when a bird leaves its nest and when it migrates or disperses (Cox et al. 2014). During this period, juveniles are relatively immobile and susceptible to predation and exposure to adverse environmental conditions (Anders et al. 1997, Kershner et al. 2004, King et al. 2006, Yackel Adams et al. 2006, Ausprey and Rodewald 2011, Dybala et al. 2013). Furthermore, variation in juvenile traits at fledging may be influenced by environmental conditions such as parental incubation, ambient temperatures, precipitation, predation risk, and food quality and abundance (Remeš and Martin 2002, Searcy et al. 2004, Brouwer et al. 2014, Kasprzykowski et al. 2014, Wada et al. 2015). If juvenile phenotypic traits influence post-fledging survival, then fledgling survival is expected to be, in part, a function of carryover effects from the nestling phase. Carryover effects are well documented across other stages of songbird

life history (e.g. wintering to breeding season, Marra et al. 1998, Robb et al. 2008, Risely et al. 2013), but comparatively little is known about the transition from the pre- to post-fledging period (Vitz and Rodewald 2011).

I examined the influence of carryover effects of nestling body condition and wing development on post-fledgling survival in a Neotropical migratory songbird, the Dickcissel (*Spiza americana*). Better body condition is thought to benefit fledglings by buffering them from the elements, and providing energy reserves in times of starvation or adverse environmental conditions (e.g. Magrath 1991, Anders et al. 1997, Ausprey and Rodewald 2011, Naef-Daenzer et al. 2001, Vitz and Rodewald 2011, Maness and Anderson 2013). Likewise, the development of wing and body feathers may provide insulation from the elements and a means of evading and hiding from predators via sustained flight(s) or wing assisted running (Birkhead 1977, Verbeek 1995, Dial et al. 2006, Morrison et al. 2009, Martin 2015). I also used automated radio-telemetry systems to examine associations between fledgling phenotypic traits and activity rates. Activity rates are an indicator of mobility, and should reflect a fledgling's ability to avoid sources of mortality, particularly predation. Though alternatively, activity levels may reflect a fledgling's probability of being detected and eaten by a predator, a phenomena documented in other life history stages of birds and in other taxa (e.g. Skelly 1994, Martin et al. 2000). Lastly, I examined post-fledging cause-specific mortality to determine the relative influence and mechanistic survival benefit each trait provides against different sources of mortality.

Specifically, I asked: (1) Do body condition and wing development at fledging predict juvenile survival and activity rates during the post-fledging period? And if so, are there specific ages at which these traits confer a survival advantage? (2) What is the relative influence of body

condition and wing development on cause-specific mortality (predation and exposure to the elements) of fledglings?

2.3 Methods

Focal Species and Study Sites

The study species for my research was the Dickcissel, a polygynous Neotropical migratory songbird breeding the grasslands of the Midwestern United States (Temple 2002). Dickcissels are a small-to-medium sized (19 to 35 g) passerines that commonly breed on my study sites (>50 males per plot). In my study system, Dickcissel initiate breeding in late May and finish initiating nests in mid-July. Females lay clutches of 2 to 6 eggs (average 4 eggs), which are incubated for ~11 days, and young are cared for in the nest by both adults for 7 to 9 days.

I conducted fieldwork from 2014-2015 on two grassland sites (~15km apart) ranging from 129.5 ha and 259ha located in central IL, USA. Grasslands were converted agricultural land under the jurisdiction and active management (burns conducted every 3 years) of the Illinois Department of Natural Resources. These grasslands consisted of a mosaic of warm and cool season grasses and forbs, exotic invasives such as Canada Thistle (*Cirsium arvense*), and wetland areas. Additionally, grasslands contained and were surrounded by agricultural lands consisting of feed corn, soybean, and wheat crops.

Locating Nests, Banding, Measuring, and Attaching Radio-transmitters to Nestlings

I located Dickcissel nests from May through August in 2014 and 2015 by systematically searching vegetation and observing behavioral cues of adults. I inspected nests every 3 to 6 days, and every 1 or 2 days as the predicted day of fledging approached. On the day of fledging (day 7 or 8), I banded nestlings with a metal U.S. Geological Survey leg band and a unique combination of plastic color bands. For each banded nestling, I documented weight via a digital spring scale,

measured tarsus length with calipers, obtained ~20µL of blood via brachial venipuncture (which was then stored in lysis buffer for later analysis), and photographed the extended right wing with a digital camera (Fig. 2.1). I randomly selected 1-3 nestlings per brood and fitted them with a 0.7g radio transmitter with a 12cm whip antenna and 42 to 60 days of battery life (Lotek, Newmarket, Ontario, Canada; and JDJC Corporation, Fisher, Illinois). Transmitters were attached with an adult size (determined via Naef-Daenzer 2007) figure-eight leg harness constructed with elastic beaded cord (Rappole and Tipton 1991). I glued synthetic fabric underneath the transmitter to keep transmitters from falling off until fledglings grew into their adult size harness, at which point the synthetic fabric flattens, falls off, or is preened off by fledglings (T. Jones, *personal observations*). I radio-tagged more than one nestling from broods as past rates of nest predation on Dickcissels indicated that sample sizes would be insufficient if I only selected one individual per nest (e.g. Berkeley et al. 2007, Suedkamp Wells et al. 2007). Fledgling blood was sent to Animal Genetics Inc. (USA) for sex determination.

Manual Radio-tracking

To estimate fledgling survival, I located radio-tagged birds once every 1 to 3 days during the first week post-fledging, and once every 1 to 5 days until fledglings dispersed, died, or until the radio-transmitter's battery died. I located fledglings by homing in on their signal with a three-element Yagi antenna and a receiver until individuals were spotted. If I was unable to detect a signal near the last documented location, I spent at least 30 minutes walking around in adjacent habitat (<400m radius) in attempt to relocate individuals. Fledgling locations were georeferenced (Garmin GPSMAP64).

For each fledgling, I assigned one of four different fates: (1) Survived—fledgling lived until it left the study site; (2) Died due to predation—its transmitter was found next to remains or

had obvious signs of damage caused by a predator (e.g. tooth or beak marks, harness material chewed through), I tracked its signal back to a predator, or its transmitter signal was lost prior to ages at which the fledgling could leave the area or disperse; (3) Died due to exposure-I found a fledgling dead with the transmitter still attached and no signs of predation; or (4) Unknown—for any reason I felt unsure that a fledgling had died or moved off when a signal was lost or transmitter was found on the ground. Though fledgling death due to starvation has been documented in previous post-fledging studies (e.g. Yackel Adams 2006), I found no emaciated fledglings in my study system. Therefore, I did not include starvation as a source of mortality for my study. Fates were determined using hand-tracking, visual observations, and ARTS data.

Automated Radio-tracking

I used established automated radio-telemetry systems (ARTS) at both study sites to sample activity rates of radio-tagged fledglings continuously across the post-fledging period. ARTS consisted of five to eight radio-telemetry towers, each with an automated receiver unit (ARU) connected to six, 3-element Yagi antennas. The azimuths of the six antennas were spaced by 60° to give 360° coverage. Each ARU was programmed to tune at intervals of 2-3 minutes to the radio frequency of each Dickcissel transmitter. The ARUs provide signal strength data for each antenna which can then be used to estimate the bearing of the transmitter from the ARU, as well as activity.

When a radio-tagged individual moves the orientation of its transmitter antenna changes. When a transmitter antenna moves, the ARU's antennas detect, at least, a change in signal strength and often a change in the bearing (Sperry et al. 2013, Steiger et al. 2013, Ward et al. 2013, Ward et al. 2014). Thus, to quantify activity, I used changes in estimated signal strength and bearing between subsequent detections to determine if a bird moved since it was last

detected. To determine thresholds for defining movement, I determined the background variation in bearing and signal strength of a stationary transmitter and in some cases where individuals were known to have died. I considered changes in signal strength >3.0 dBm in association with changes in bearing >1.8º to be indicative of movement. I then used the number of times a fledgling moved divided by the total number of detections in an hour, then averaged across all hours of a day to derive activity rates (movements/hour/day) for each radio-tagged individual. In previous studies, activity thresholds were set higher to detect whether an individual moved between trees or bushes (Steiger et al. 2013, Ward et al. 2013, Ward et al. 2014). In this study, however, I used lower thresholds to quantify smaller-scale movements.

Statistical Analyses

To characterize condition I used the residuals from a linear regression of nestling tarsus and body mass ($P<0.0001$, $r^2=0.45$) as a condition index (Vitz and Rodewald 2011) with the assumption that positive residuals indicate better body condition than at average. To characterize wing development from photographs, I used the measurement tool in ImageJ (Rasband 1997-2015) to estimate the proportion of the feather emerged from the shaft relative to the entire length of the feather (emerged + shaft) for each primary feather. I then averaged primary feather emergence values for each individual to derive an estimate of wing development (Figure 2.1)

I used multi-state models in program MARK (White and Burnham 1999) to estimate fledgling probabilities of mortality/survival. Multi-state models estimate survival (ϕ) while accounting for resighting probabilities of individuals (p), and also allow the increased flexibility of incorporating discrete states for capture-resighting occasions and accounting for transition probabilities among states (Ψ), uncertainty in state membership for occasions when an individual was not observed, and estimates of survival and resighting probability that are specific to each

state. I assigned each individual observation to one of four discrete states: alive (present on site or dispersed), dead due to exposure, dead due to predation, and not observed. For all models, I fixed the survival parameter at one, the transitional probability from a dead state to an alive state and dead state to a dead state at zero (i.e. death as an "absorbing state"), and based my inferences on the transition probabilities from alive to dead due to exposure or due to predation.

Age is the main predictor of fledgling survival in post-fledging studies (Cox et al. 2014). Thus, before examining effects of body condition and wing development on post-fledging survival, I refined my models by determining how probability of fledgling mortality was best described by age. I examined five models in which fledgling mortality was linear (most parsimonious trend, with fledgling mortality expected to decrease with age) across specified age classes (fledgling ages grouped to represent distinct stages of fledgling growth, with short periods of more rapid growth followed by longer, slower sustained growth) (e.g. Yackel Adams et al. 2006, Vitz and Rodewald 2011). The best supported age model included six age classes (ages 0, 1, 2, 3, 4-11, 12+ post-fledging) which were used in all subsequent models.

To examine the influence of carryover effects on post-fledging survival, I added nestling condition and wing development as single and additive covariates in accordance with alternative *a priori* hypotheses in which: (1) covariate effects influence mortality for (a) all days post-fledging; or (b) the first four days post-fledging; and (2) covariate effects influence (a) both sources of mortality; or (b) wing development influences mortality due to predation and condition influences mortality due to exposure. I also examine tarsus as a single covariate effect to insure that fledging body size alone is not an important predictor of post-fledging survival. Additionally, I ran models assessing the importance of brood size, fledge date, ordinal date, and fledgling sex and compared them to my top mortality model. I ranked models using an

information-theoretic approach accounting for small sample sizes (AIC_c), focusing on both AIC_c differences (ΔAIC_c) and Akaike weights (w_i) (Burnham and Anderson 2002). I calculated cumulative survival probabilities by multiplying daily survival estimates up to a given day; I focused on cumulative survival up to day 4 and up to day 36 post-fledging.

During my study 37 of the 102 radio tagged fledglings also had at least one other sibling that was tagged. Radio-marking multiple fledglings from the same brood has the potential to introduce non-independence if those fledglings are more likely to experience similar fates than those from different broods. Unfortunately, multi-state models in MARK cannot incorporate random effects (such as random effect statements in other statistical programs; which I use in other analyses of this thesis) which could account for non-independence amongst fledglings from the same brood. I therefore examined the potential for non-independence of brood mate fates using a modified chi-square test which examined the number of young surviving a 21-day period (an age by which most fledglings become independent from adults) as a function of brood identity (Wiens et al. 2006). I found no evidence of non-independence in fates of fledglings from the same brood (X^2= 4.24, $\hat{c}$<1). Thus, I retained data from all fledglings for subsequent analyses. I also evaluated multicollinearity among covariates and did not include highly correlated variables ($|r| > 0.40$) in the same model.

I examined associations between activity rates of fledglings (n=51), and their age, condition, and wing development during the first six days of the post-fledging period using generalized linear mixed models (Proc Glimmix, SAS Institute, 1990). I used a binomial distribution and logit link function with activity rate (average proportion of observations in which movements were documented per hour, per day) as the response variable, and fixed effects of a fledgling trait (wing development or condition), age, and age by trait interaction. To account

for issues of non-independence with multiple observations per fledgling and fledglings from the same brood I included nest and individual ID as random effects. The number of ARU observations per bird per hour ranged from 2 to 30; because I did not want to give equal weight to activity rates based on 2 and 30 observations, I used the number of observations in each hour as a weighting factor for my analysis. Activity rates were not included as covariates in the multi-state survival models as I lacked data for half of the fledglings; technical issues with telemetry systems and early fledgling death made it impossible to estimate activity for all individuals.

2.4 Results

Fledgling Survival and Mortality- I monitored the survival of 104 Dickcissel fledglings (51 females, 47 male, and 6 of unknown sex), of which 34 (33%) survived until they left the study site or their transmitter battery died. Of the 68 confirmed mortalities, 43 (63%) died within the first four days of fledgling, 18 (27%) died within 4-11 days of fledging, and 7 (10%) died 12 or more days after fledging. Two (1.9%) fledglings were assigned unknown fates and excluded from survival models. No birds were confirmed dead after surviving the first 36 days post-fledging. Of the 68 confirmed mortalities, 63% were due to predation and 37% were due to exposure. Probability of survival was lowest across the first four days and increased with age until approaching 100% after 12 days post-fledging (Figure 2.2). Cumulative survival was 49% for the first four days after fledging, and 29% through day 36.

Factors influencing post-fledging mortality- Daily post-fledging probability of mortality was best explained by age and with body condition and wing development differentially influencing cause-specific mortality for the first four days (Table 2.1). Better body condition was associated with decreased probability of mortality due to exposure, whereas more developed wings were associated with decreased probability of mortality due to predation. Body condition

and wing development were most influential during the first four days post-fledging, with the effects of body condition and wing development becoming minimal on day three post-fledging (Fig. 2.3). My 5th ranked model provided further support for these findings, as when covariate effects of body condition and wing development were modeled to effect mortality due to predation and exposure respectively, no relationships with post-fledging mortality were found (Condition-Predation: β = -0.106, CI= -0.363 to 0.151; Wing Development-Exposure: β = 0.024, CI= -3.783 to 3.830); and removing such effects resulted in my top ranked model. We also found no relationship between tarsus (body size) and probability of post-fledging cause-specific mortality (Table 2.1, 2.2). Models incorporating Julian date, sex, fledge date, and brood size at fledging received less support than our top models incorporating condition and wing development (Table 2.1). Fledgling probability of mortality due to exposure increased with brood size, but decreased with later fledging and ordinal dates, while no relationships between probability of mortality due to predation and each variable were found; and I found no relationship between fledgling sex and fledgling cause-specific mortality (Table 2.2).

Early Post-fledging Activity Rates- The effect of body condition at fledging on activity rates was dependent on age (β = 0.013, P = 0.08). Regardless of condition, fledglings shared similar activity rates through the first 3 days post-fledging, but individuals which fledged in better condition became more active than their counterparts in subsequent days (Fig. 2.4). Fledgling activity rates increased with age (β = 0.078, $P < 0.0001$) and individuals with more developed wings at fledging were more active throughout the early post-fledging period (β = 1.246, P = 0.06, Fig. 2.4). The interaction of age and wing emergence was not included in my model as it was non-significant (P = 0.7769).

2.5 Discussion

I identified pre- to post-fledging carryover effects in which better body condition and more advanced wing development at fledging confers survival benefits for fledglings. Survival benefits for each trait, however, depended on the specific source of mortality and had the greatest influence on fledgling mortality during the first four days post-fledging when mortality rates were highest. Individuals that fledged in better body condition were less likely to die from exposure whereas those with more developed wings were less likely to be preyed upon. The presence and relative influence of pre- to post-fledging carryover effects across bird taxa producing altricial young remains uncertain, however, and calls for further inquiry.

My activity analyses suggest potential mechanisms by which more developed wings confer survival advantages for fledglings. Though I did not directly quantify how well fledglings could move or fly, fledglings with more developed wings moved with greater frequency during the post fledgling period (Fig. 2.4). Individuals with more developed wings also flushed, and exhibited longer flights sooner after fledging (T. Jones, *personal observations*). Past research also documents positive association between increased locomotor ability and advanced wing development (e.g. Dial et al. 2006). Thus, this association suggests more developed wings allow fledglings to better escape predation by avoiding, hiding from, or directly evading predators.

Anti-predator benefits of wing development in the face of high predation rates (nearly twice as many fledgling died due to predation than exposure) should ultimately drive Dickcissel nestlings to invest more in wing growth than improved body condition, resulting in tradeoffs between the two traits. Contrary to past studies (Coslovsky and Richner 2011, Cheng and Martin 2012), however, I found no apparent tradeoff between wing development and body condition in my study system (Fig. 2.5). My results therefore raise not only the question of why tradeoffs

between the traits do not exist, but why so much variation in body condition and wing development at fledging exists amongst juvenile Dickcissels. I suspect that variation in factors such as energy available for growth (Searcy et al. 2004), interactions amongst traits (e.g. Nijhout and Emlen 1998) and genetics may be altering or masking baseline growth strategies of nestlings. The lack of a tradeoff also makes it unclear as to how variation in nestling wing development and body condition are expected to change along a cline whereby rates of predation and the threat of death due to exposure also change. Indeed, more experimental and comparative studies are needed to better understand baseline nestling growth strategies and interactions amongst nestling wing development, body condition, locomotor ability, and variation in post-fledging cause-specific mortality.

My findings corroborate an important assumption of comparative studies linking juvenile development and post-fledging survival with latitudinal variation in life history strategies of birds; in particular, that variation in juvenile characteristics at fledging affect fledgling survival (Martin 2014, 2015). Such studies have focused on this phenomena across species, but my findings describe similar associations within species, and to my knowledge provides the first evidence of wing development affecting post-fledging survival in a songbird. Thus, my research adds further evidence as to the importance of post-fledging survival in regards to life history evolution in songbirds.

The post-fledging period is a critical time for songbirds and is associated with increased mortality (Cox et al. 2014), however, my results suggest that heterogeneity in individual mortality risk is partially driven by pre- to post-fledging carryover effects of nestling phenotypic traits. Thus, understanding constraints and tradeoffs faced by young and parents during the nestling stage and how they carryover into subsequent stages has implications not only for

understanding avian life histories but also for conservation and management. Indeed, the percentage of young achieving stages of development that better prepare them for surviving the critical four days after fledging may be a reflection of the quality of habitat in which they nested. Nestlings, may therefore, act as an important biological index by which lower percentages of high-quality nestlings highlight areas of poor quality. In turn, such areas should be the focus of future investigations into interactions among avian breeding ecology, post-fledging ecology, and habitat management.

2.6 Figures and Tables

FIGURE 2.1. Variation in wing development (quantified value in upper right corner of each photo) of nestling Dickcissels just prior to fledging in grasslands of eastern Illinois, USA, 2014-2015. Wing development was quantified using the measurement tool in ImageJ to calculate the proportion of the feather emerged from the shaft to the entire length of the feather (emerged + shaft) for each primary feather. Emergence values for each individual were then averaged to derive a development estimate.

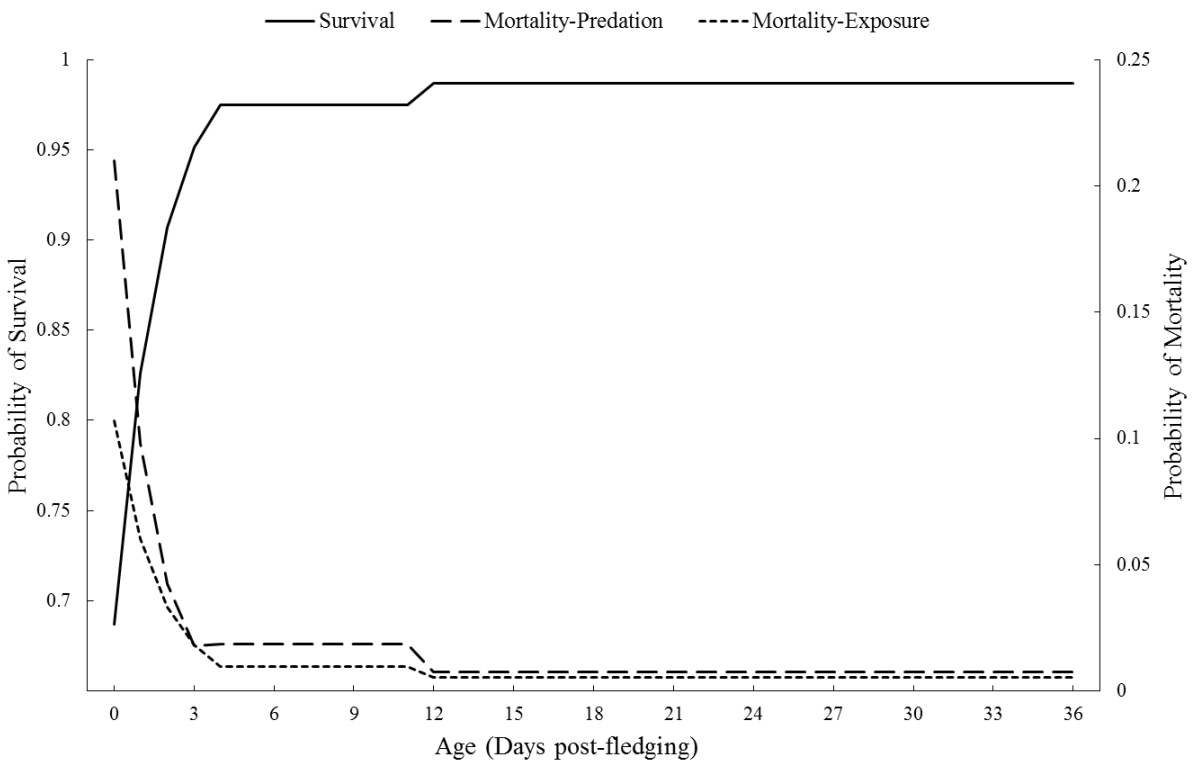

FIGURE 2.2. Post-fledging probabilities of survival, of mortality due to exposure, and mortality due to predation in relation to age of fledgling Dickcissels (n=102) in grasslands of eastern Illinois, USA, 2014-2015.

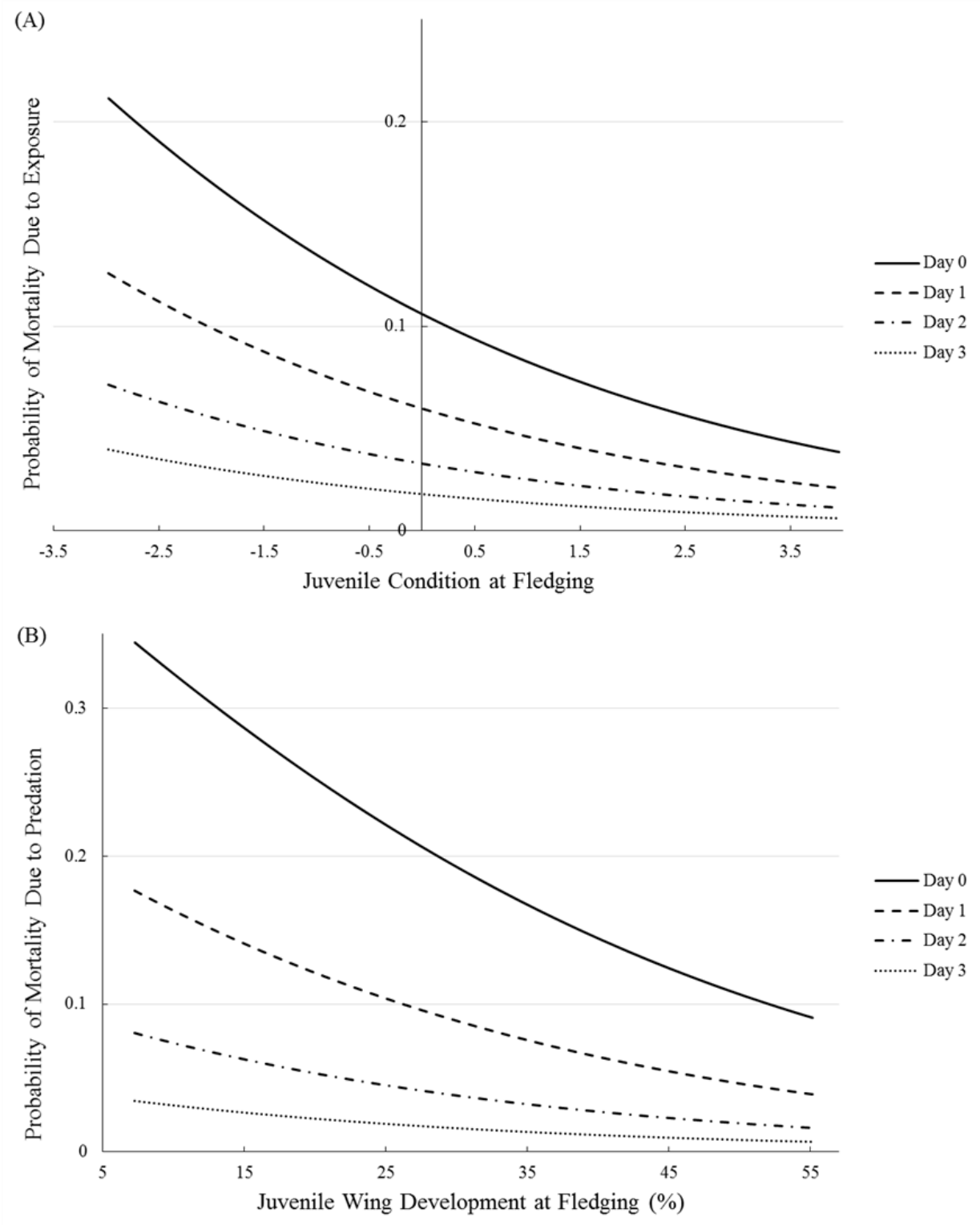

FIGURE 2.3. Probability of mortality due to (A) exposure and (B) predation in relation to carryover effects of nestling body condition and wing development (respectively) at fledging for juvenile Dickcissels (n=102) during the early post-fledging period in grasslands of eastern Illinois, USA, 2014-2015.

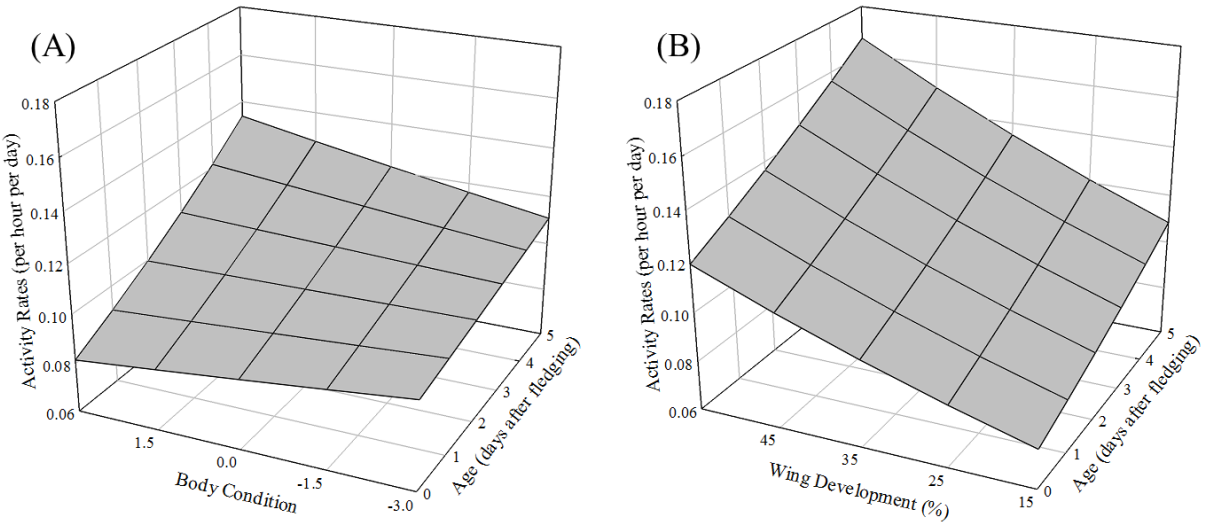

FIGURE 2.4. Relationship of post-fledging activity rates for juvenile Dickcissels (n=51) in relation to age and (A) juvenile body condition or (B) wing development at fledging of during the early post-fledging period in eastern Illinois, USA, 2014-2015.

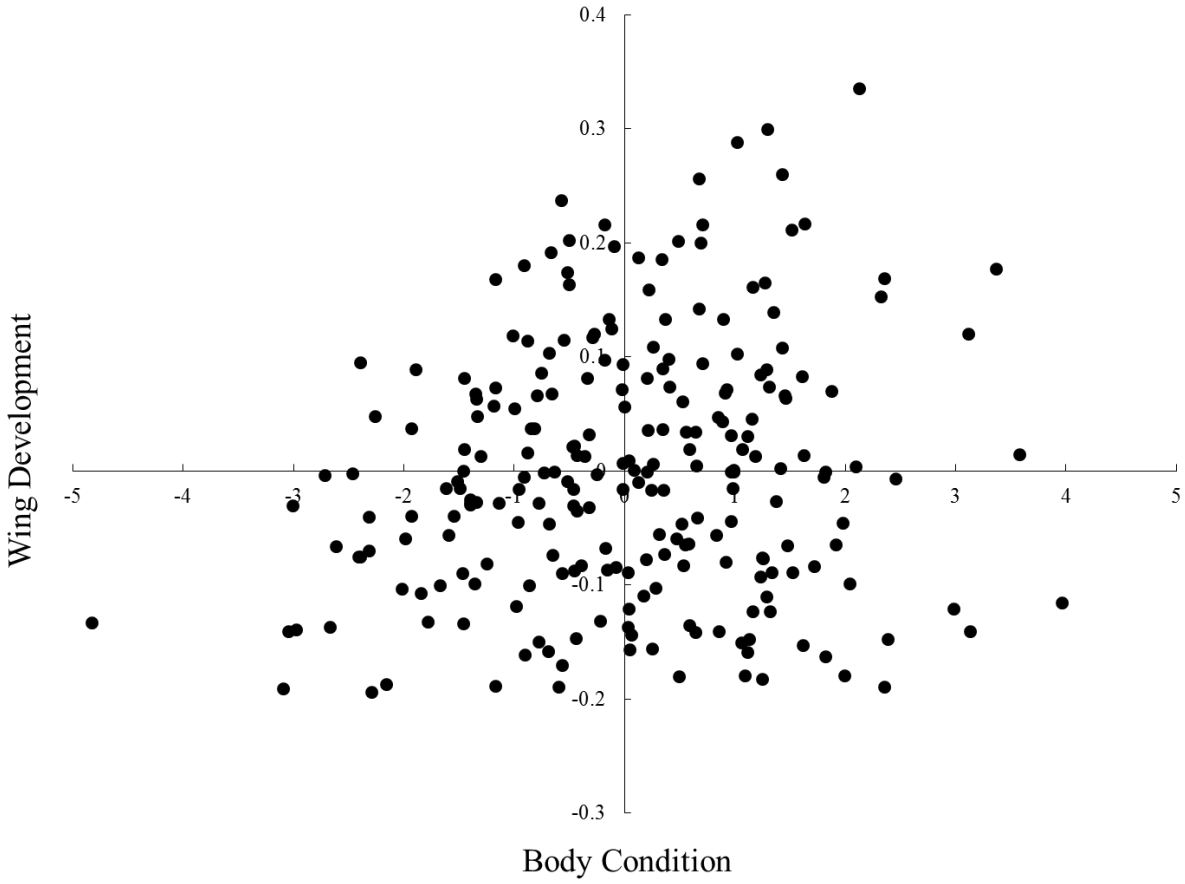

FIGURE 2.5. Relationship between of body condition and wing development (corrected for body size) at fledging for juvenile Dickcissels (n= 237) in eastern Illinois, USA 2014-2015.

TABLE 2.1. Results from multi-state models examining the factors influencing post-fledging mortality of Dickcissels (n=102) in grasslands of eastern Illinois, USA, 2014-2015. Models are based on *a priori* hypotheses of factors impacting mortality, where mortality was cause-specific (predation and exposure, unless otherwise specified), covariate effects were modeled for one or both sources of mortality, and for the four youngest age classes (early part of the post-fledging period) or all age classes (entire post-fledging period).

Model	ΔAIC_c	w_i	k	Deviance
Age + Condition (exposure)$_{early}$ + Wing (predation)$_{early}$	0.00	0.37	7	485.43
Age + Condition (exposure)$_{entire}$ + Wing (predation)$_{entire}$	1.01	0.22	7	486.44
Age + Broodsize$_{early}$	2.41	0.11	7	487.84
Age	3.16	0.08	5	492.68
Age + Condition$_{early}$ + Wing$_{early}$	3.45	0.07	9	484.77
Age (mortality sources pooled rather than cause-specific)	4.40	0.05	3	497.64
Age + Fledgedate$_{entire}$	4.28	0.04	7	489.83
Age + Condition$_{entire}$ + Wing$_{entire}$	5.01	0.03	9	486.32
Age + Sex$_{entire}$	5.99	0.02	7	491.59
Age + Tarsus$_{early}$	6.16	0.02	7	491.59
Ordinal Date	81.42	0.00	5	570.94
Constant Survival	110.12	0.00	2	605.71

Age: Refers to top-ranked age model with age classes: 0, 1, 2, 3, 4-11, and 12+ days post-fledging
^{entire}Effect was modeled for all age classes
^{early}Effect was modeled for age classes, 0, 1, 2, and 3

TABLE 2.2. Associations of model effects and juvenile post-fledging daily probability of cause-specific mortality (predation or exposure) for fledgling Dickcissels (n=102) in grasslands of eastern Illinois, USA, 2014-2015. Beta values were derived from the highest ranked model for which each effect is included.

Effect	β	SE	95% CI
Body Condition at Fledging- Exposure	-0.274	0.170	-0.608 to 0.060
Wing Development at Fledging- Predation	-3.470	1.737	-6.873 to -0.066
Age- Exposure	-0.623	0.114	-0.847 to -0.400
Age- Predation	-0.895	0.131	-1.151 to -0.638
Broodsize- Exposure	0.395	0.176	0.050 to 0.740
Broodsize- Predation	-0.023	0.156	-0.328 to 0.282
Fledge Date- Exposure	-0.024	0.014	-0.052 to 0.004
Fledge Date- Predation	0.002	0.011	-0.020 to 0.024
Sex- Exposure	-0.114	0.355	-0.811 to 0.582
Sex- Predation	0.299	0.269	-0.227 to 0.826
Tarsus- Exposure	0.008	0.052	-0.094 to 0.111
Tarsus- Predation	-0.050	0.050	-0.148 to 0.049
Ordinal Date- Exposure	-0.043	0.012	-0.067 to -0.019
Ordinal Date- Predation	-0.034	0.009	-0.051 to -0.016

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CHAPTER 3: Post-fledging Habitat Use in the Dickcissel

3.1 Abstract

Management of many species is currently focused on specific life history stages which are not the crucial period in which management approaches are needed. In birds, management of breeding habitat is generally focused on the pre-nesting and nesting stages, while the post-fledging stage may be the most critical for conservation. From 2014-2015, I documented post-fledging habitat use of Dickcissels (*Spiza americana*) inhabiting grasslands of central Illinois, USA. I examined which vegetation characteristics were used by fledglings and whether such characteristics were associated with fledgling survival. I also compared habitat use of fledglings to nesting habitat of breeding adults. I found that fledglings used areas of greater vegetation density (vegetation that was taller, denser, and provides more concealment for birds); fledglings using denser areas of habitat during the early part of the post-fledging period also had higher post-fledging survival prospects. Fledgling habitat use was age and mobility dependent, with fledglings using denser vegetation early in the post-fledging period, but using even denser vegetation once they aged and became more mobile (days 4 to 11 post-fledging). Habitat used by fledglings did not differ from nesting habitat. My results highlight variation in habitat needs both within and amongst life history stages of birds; and during what is often considered the most critical life stage for birds, specific micro-habitat characteristics are selected for. Therefore, conservation agencies should strive to provide and maintain diverse vegetation structure throughout grassland landscapes in order to provide suitable habitat for various periods of a bird's life.

3.2 Introduction

Current management of many species is based on limited information and is focused on specific life history stages (Crouse et al. 1987, Christensen et al. 1996) that are not the crucial period in which management approaches are needed. Management for birds is no exception, as efforts have primarily focused on aspects of avian pre-nesting and nesting stages, whereas one of the least studied life history stages—the post-fledging period—may be the most important for avian conservation (Cox et al. 2014). Defined as the time between when a bird leaves its nest and when it migrates or disperses, the post-fledging period is often associated with high rates of fledgling mortality (Anders et al. 1998, Vega Rivera et al. 1998, Berkeley et al. 2007, Vitz and Rodewald 2011). Since fledgling survival is thought to play a critical role in avian population dynamics (Anders et al. 1997, Anders and Marshall 2005), improving post-fledging survival prospects may be critical for bird conservation.

Fortunately, research on post-fledging ecology suggests that management of breeding habitats may improve fledgling survival (Cox et al. 2014). Fledglings often use and have higher survival rates when using areas of denser vegetation (Anders et al. 1998, King et al. 2006, Berkeley et al. 2007, Jones and Bock 2005, Rush and Stutchbury 2008, Fisher and Davis 2011). Such areas are thought to benefit fledgling survival by providing better cover from predators and acting as a thermal refuge during period of adverse environmental conditions (Anders et al. 1998, King et al. 2006, Cox et al. 2014). In theory, managing for such dense areas should therefore aid post-fledging survival rates. Whether this is true for all avian species remains unclear, however, and requires further investigation.

For management of avian habitats to be effective, all stages of the annual life cycle must be considered (Norris and Marra 2007). In the case of many migratory species, this includes

adult, nesting, and fledgling life history stages. Management agencies frequently consider fledgling and adult breeding habitat to overlap, but fledgling habitat use often differs markedly from that of adult breeders (Anders et al. 1998, King et al. 2006, Jones and Bock 2005, Vitz and Rodewald 2010). Furthermore, in cases where adult and post-fledging habitat appear to be similar, there also may be subtle differences. Identifying such differences may be crucial for effective conservation. Unfortunately, while many studies have documented habitat use of fledglings, far fewer have compared such parameters to adult habitat use (e.g. nest sites; Anders et al. 1998, Fisher and Davis 2011).

I investigated habitat use of fledgling and adult Dickcissels (*Spiza americana*) inhabiting grasslands of central IL, USA. Dickcissels are part of a community of grassland birds which have experience the steepest population declines of any group of birds in recent decades (Brennan and Kuvlesky 2005). Given that current management of grassland landscapes primarily focuses on adult breeding habitat (e.g. Johnson et al. 2004), incorporating post-fledging habitat use of grassland species such as the Dickcissel into management plans may be important for effective conservation. Furthermore, determining how fledgling habitat use ultimately influences survival may aid conservation efforts by elucidating mechanisms of population declines. Therefore, the objectives of my study were to (1) examine and compare habitat use of fledgling and breeding adults, and (2) examine habitat use in relation to fledgling survival.

3.3 Methods

Focal Species and Study Sites

A polygynous migratory passerine, Dickcissels breed in the grasslands of the Midwestern United States (Temple 2002). Small-to-medium sized (19 to 35 g), Dickcissels commonly breed on my study sites (>50 males per plot) and initiate breeding in late May and finish laying their

last clutch of eggs in mid-July. Females incubated clutches of 2 to 6 eggs (average 4 eggs) for ~11 days, and young are cared for 7 to 9 days by both adults.

In 2014-2015, I studied Dickcissels on two grassland sites (~15km apart) located in Central IL, USA; ranging from 129.5 ha and 259 ha in size. Previously converted from agricultural lands, these grasslands are part of a State Acres for Wildlife Enhancement (SAFE) program under the jurisdiction (burns conducted every 3 years, mowing, spraying of herbicides) and management of the Illinois Department of Natural Resources. Each grassland consists of a mosaic of warm and cool season grasses and forbs, exotic invasives such as Canada Thistle (*Cirsium arvense*), and wetland areas. Both grasslands also contained and were surrounded by agricultural lands which rotate feed corn, soybean, and wheat crops.

Locating Nests, Banding, Measuring, and Attaching Radio-transmitters to Nestlings

From May through August of 2014 and 2015, I located Dickcissel nests by systematically searching vegetation and observing behavioral cues of adults. Nests were visited every 3 to 6 days, and every 1 or 2 days as the day of fledging approached. On the day nestlings were predicted to fledge, I capture nestlings and banded them with a metal U.S. Geological Survey leg band and a unique combination of plastic color bands. Additionally, I attached a 0.7g radio-transmitter with a 12cm whip antenna and 42-60 days of battery life (Lotek, Newmarket, Ontario, Canada; and JDJC Corporation, Fisher, Illinois) to 1-3 randomly selected nestlings per brood. I attached transmitters using and adult size backpack (determined via Naef-Daenzer 2007) figure-eight leg harness constructed with elastic beaded cord (Rappole and Tipton 1991). To prevent adult size harnesses from falling off of fledglings, I glued a synthetic fabric underneath transmitters which eventually falls off, and/or is preened off by fledglings (T. Jones, *personal observations*) once they are adult sized. High rates of post-fledging mortality for Dickcissels

(e.g. Berkeley et al. 2007, Suedkamp Wells et al. 2007). dictated that I radio-tag more than one nestling from some broods so as to collect sufficient samples sizes of fledgling habitat use.

Radio-tracking

I used a three-element Yagi antenna with a receiver to home in on and document the exact location of fledglings every 1 to 3 days during the first week post-fledging, and once every 1 to 5 days until fledglings left the study sites, died, or until the radio-transmitter's battery died. When I was unable to detect a signal near a fledgling's last documented location, I searched the adjacent habitat (<400m radius) for at least 30 minutes in an attempt to pick up a signal. I used a GPS unit (Garmin GPSMAP64) to georeferenced all fledgling locations.

Vegetation Measurements

I collected vegetation measurements in 1 m^2 quadrats (Small et al. 2015) at each fledgling location, a paired random location, and each fledgling's nest location. I recorded the average vegetation height, total percent cover of vegetation (i.e. "canopy cover"), a robel value (visual obstruction at a distance of 1m and height of 1m above the ground, with the value recorded being the fists height at which the pole was 50% concealed by vegetation) and percent concealment (the average percent of the bird or nest concealed from each point a robel sample was taken) for each vegetation plot. Random plots were located within 15m of fledgling locations 1 to 3 days after fledging, within 25m 4 to 13 days after fledging, and with 50m of fledgling locations 14+ days after fledging. Similar to Fisher and Davis (2011), this approach accounts for the increasing mobility of fledglings with age, and reflects the increased area of habitat that they can reach and have the potential to use. Vegetation was sampled 1 to 4 weeks after fledglings left the area, with fledgling and paired random sites sampled on the same day.

Fledgling Fate

I assigned each fledgling one of three fates: (1) Survived—fledgling lived until it dispersed; (2) Died— fledgling was found dead with the transmitter still attached, its transmitter was found next to remains or had obvious signs of damage caused by a predator (e.g. tooth or beak marks, harness material chewed through), I tracked its signal back to a predator, or its transmitter signal was lost prior to ages at which the fledgling could leave the area or disperse; or (3) Unknown—for any reason I felt unsure that a fledgling had died or moved off when a signal was lost or transmitter was found on the ground. Fates were determined using hand-tracking, visual observations, and automated radio-telemetry system data.

Data Analyses

To compare habitat of fledgling vs random locations and fledgling vs fledgling nest locations, I used two different approaches. For the first approach I examined each of the four vegetation characteristics separately using univariate models. By keeping each variable separate, I hoped to use comparisons drawn from raw numbers to provide useful comparisons for management agencies. In the second approach, I used principal component analysis (PCA, Proc Factor, SAS Institute, 1990) to reduce the dimensionality of vegetation characteristics down to one variable. I then used the new variable in a univariate model to provide more holistic and biologically meaningful results. In this way, my two analyses provide information to parties interested in a more basic or applied aspect of post-fledging habitat use.

For the univariate models, I first determined the difference between paired plots of each variable representing vegetation characteristics. Using the difference as a response variable and the intercept as the only explanatory variable, I tested whether differences in vegetation structure of fledgling and random locations were equal to zero during days 1 to 3, 4 to 11, and 12+ post-fledging (Proc Glimmix, SAS Institute, 1990). In other words, if the intercept of a model was

significantly different from zero (P near or < 0.05), then the difference between the vegetation variable for that model was considered significant. Nest ID and bird ID were included as a random factors to account for issues of non-independence between members of the same brood and multiple observations from the same individual.

I examined early fledgling habitat use in association with fledgling fate via generalized linear mixed models (Proc Glimmix, SAS Institute, 1990). I use a binomial distribution and logit link function with fledgling fate (binary, died or survived) as the response variable and a vegetation characteristic as the independent variable (one model for each variable). I constrained my models to days 1 to 3 post-fledging, as this time represents the critical part of the post-fledging period when mortality rates are highest (Chapter 2), and therefore where habitat use should have the most influence on survival. Nest ID and bird ID were included as a random factors to account for issues of non-independence between members of the same brood and multiple observations from the same individual. Fledglings with unknown fates were not included in my analysis.

3.4 Results

Habitat characteristics were measured at a total of 677 points: 323 fledgling locations, 323 random locations, and 52 nest locations of 60 different fledglings. I also examined associations amongst habitat characteristics of locations used during days 1 to 3 post-fledging and fledgling survival for 57 individuals. Though I tracked the survival of 102 fledglings, I was unable to collect vegetation for all individuals due to early fledgling death and time constraints.

For my PCA, the first principal component explained 54% of the variation (eigenvalue= 2.17) of the vegetation variables, all of which loaded positively, suggesting that the factor represented overall "vegetation density" (i.e. vegetation that is taller, horizontally and vertically

more dense, and provides more concealment for fledglings). All other factors produced from the PCA had eigenvalues less than 1 and were not used in any further analyses (Table 3.1). Young fledglings (days 1-3 post-fledging) used areas of denser vegetation compared to random areas (Table 3.2). Furthermore, the difference between vegetation density of fledgling and random locations became greater as fledglings aged (days 4-11 post-fledging, Table 3.2). No significant differences between habitat characteristics of fledgling and fledgling nest locations for all post-fledging age classes were found (Table 3.2). Fledgling survival was positively associated with denser vegetation structure during the early part of the post-fledging period ($\beta = 0.013 \pm 0.3685$ SE, P=0.047).

3.5 Discussion

During the early post-fledging period, fledgling Dickcissels preferred denser habitat which reduced their risks of post-fledging mortality. Similar to other grassland and woodland species (Anders et al. 1998, King et al. 2006, Jones and Bock 2005, Rush and Stutchbury 2008, Fisher and Davis 2011), fledglings used areas of denser vegetation as compared to random locations. Areas of denser vegetation are thought to provide better cover from predators and act as a thermal refuge, which in turn should reduce risks of primary sources of mortality and improve survival prospects (Anders et al. 1998, King et al. 2006, Cox et al. 2014). Indeed, I found a positive relationship between vegetation density and fledgling survival; suggesting that fledglings not only had access to, but used areas which aided in their post-fledging survival.

Fledgling habitat use appears to be age and mobility dependent. Early in the post-fledging period (days 1 to 3) fledglings were relatively immobile and therefore limited in areas they could reach (Fig. 3.2). Fledglings were still able to use areas of denser vegetation during this time, but as they aged (days 4 to 11) and became more mobile, they were able to reach and use areas of

even denser vegetation. After day 11 post-fledging, fledglings began to exhibit more adult like behavior and appeared to be less selective in their vegetation use.

Contrary to the majority of past research examining fledgling habitat use, I observed no significant shift in habitat use from the nesting to the post-fledging period in the Dickcissel. Though my results are consistent with some grassland songbirds (Fisher and Davis 2011), differences in nesting and post-fledging habitat use are well documented in woodland species such as the Wood Thrush (*Hylocichla mustelina*; Anders et al. 1998), Ovenbird (*Seiurus aurocapilla*; King et al. 2006, Streby and Anderson 2013), and Hooded Warbler (*Setophaga citrin*a; Rush and Stutchbury 2008). Given the consensus of preferred habitats of fledgling songbirds, the presence or absence of a nest to post-fledging shift in habitat selection appears to be related to life history characteristics of each species. For instance, grassland species such as the Dickcissel place nests in denser, more complex, and well concealed areas (Winter 1999) similar to those preferred by fledglings, while species such as the Ovenbird place nests in open understories of mature forests (King et al. 2006).

Conservation Implications

Though it has become increasingly important to understand differences in habitat requirements within and amongst avian life history stages, there remains a paucity of information for most species. In this study I observed subtle differences in habitat use that translated into increased survival prospects for fledgling Dickcissels. I was unable to determine if vegetation density influences fledgling survival by concealing fledglings from predators and/or providing them with thermal refuge, however, it is clear that dense vegetation in needed for fledglings until they mature and begin to act and use habitat like breeding adults. Furthermore, it is also clear that Dickcissels are selecting different habitat characteristics both within and amongst life history

stages. Monocultures of brome or fescue—commonly planted in converted grasslands areas similar to my study sites—with simplified vegetation often go unused or have negative impacts of Dickcissel fitness (Hughes et al. 1999), which may be due to their lack of various micro-habitats Dickcissels require throughout their and their offspring's life cycle. Conservation agencies should therefore refrain from planting such monocultures, and instead strive to provide and maintain grasslands with a more complex, heterogeneous vegetation structure—areas of sparse and dense vegetation—so that grassland birds and their offspring have access to and use suitable habitat across all of their life stages.

3.6 Figures and Tables

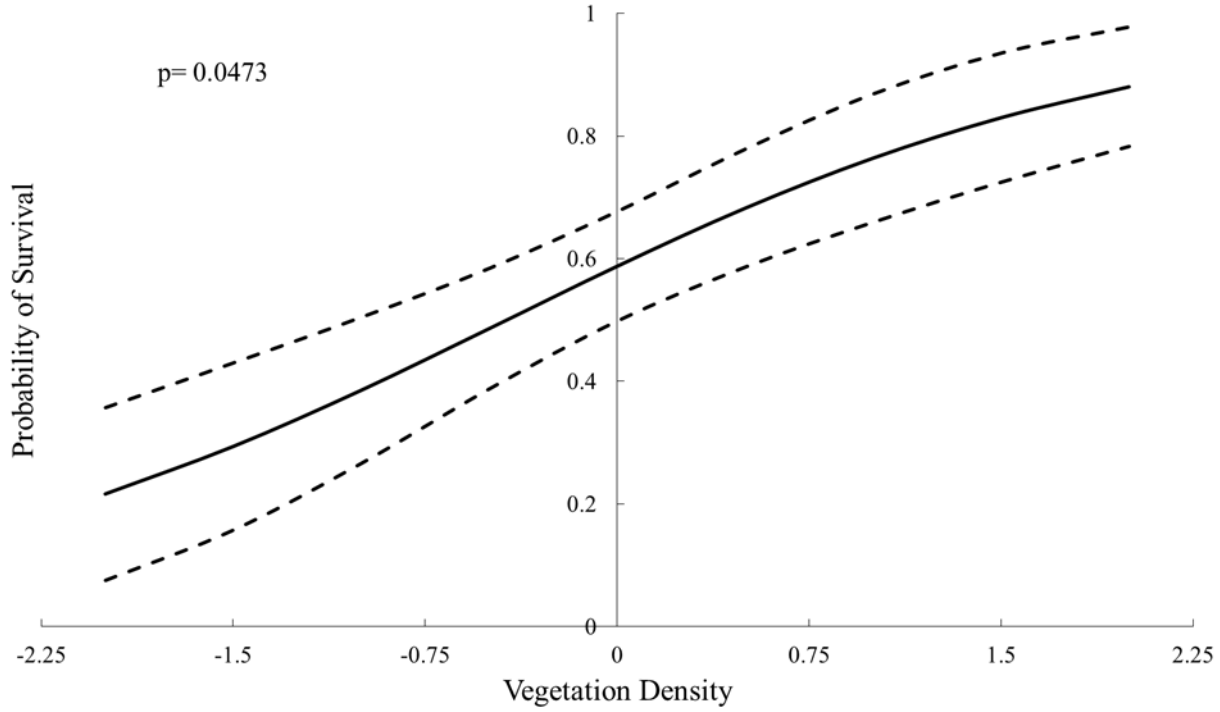

FIGURE 3.1. Association between vegetation density used by fledglings 1 to 3 days post-fledging and fledgling survival (±SE) during post-fledging period of Dickcissel (n=57) in grasslands of central Illinois, USA, 2014-2015. Vegetation structure is a factor derived from a principal component analysis of four structural features of vegetation, with more positive values representing areas with taller, denser vegetation that provides more concealment for birds.

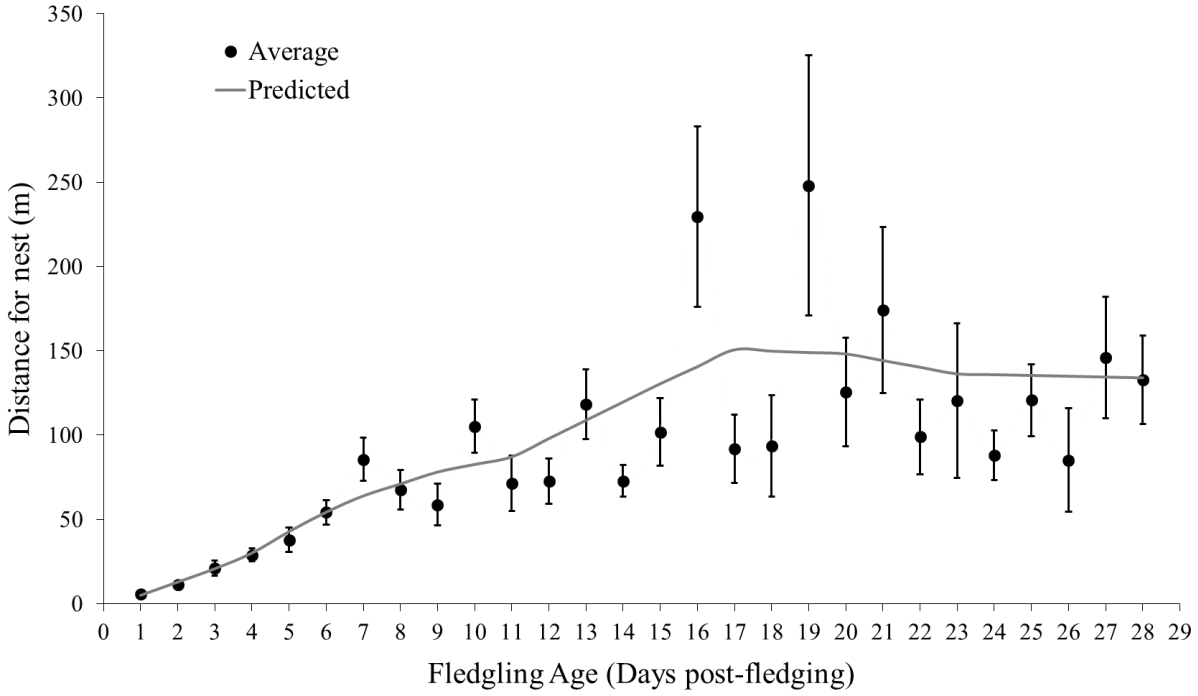

FIGURE 3.2. Average (±SE) and predicted distance of Dickcissel fledglings (n= 66) from their nest site by age (days post-fledging) in grassland of central Illinois, USA, 2014-2015. Distances from nest sites were based on GPS locations of hand-tracked fledglings and predicted values were derived from a Loess smoothing curve.

Table 3.1. Principal component analysis (PCA) of habitat characteristics reflecting vegetation structure of $1m^2$ sampling plots in grasslands of central Illinois, USA, 2014-2015.

PCA Analysis		Factor 1	Factor 2	Factor 3
Eigenvalue		2.17	0.99	0.67
Variance Explained		54.2%	25.0%	16.6%
Loadings	**Concealment (%)**	0.141	0.960	-0.230
	Cover (%)	0.467	0.142	0.873
	Robel (#)	0.620	-0.114	-0.329
	Height (cm)	0.615	-0.213	-0.279

Table 3.2. Differences in vegetation density (the primary factor derived from a principal components analysis) and the characteristics comprising vegetation density between fledgling and paired random locations, and fledgling and fledgling nest locations, during days 0-3, 4-11, and 12+ post-fledging. Vegetation was sampled in grasslands of central Illinois, USA, 2014-2015.

Fledgling Used vs Unused Locations								
Vegetation Characteristic	Fledgling Locations		Random Locations		Mean Difference Fledgling– Random	SE (Diff)	t	*P*
	Mean	SE	Mean	SE				
Days 0-3 Post-fledging								
Vegetation Density	**-0.106**	**0.097**	**-0.282**	**0.100**	**0.1880**	**0.062**	**3.08**	**0.015**
-Average Height (cm)	57.856	2.413	53.663	2.490	3.836	1.735	2.21	0.058
-Total Cover (%)	73.020	2.085	72.163	2.128	0.857	1.527	0.56	0.590
-Concealment (%)	78.000	2.021	70.555	2.196	7.660	2.282	3.36	0.010
-Robel (#; density)	3.817	0.214	3.413	0.221	0.402	0.166	2.43	0.041
Days 4-11 Post-fledging								
Vegetation Density	**0.336**	**0.094**	**-0.068**	**0.094**	**0.3985**	**0.074**	**5.35**	**0.003**
-Average Height (cm)	66.731	2.545	60.068	2.518	7.059	1.833	3.85	0.012
-Total Cover (%)	78.748	1.498	73.985	1.933	4.763	1.726	2.76	0.040
-Concealment (%)	79.210	1.741	66.281	2.250	13.421	2.009	6.68	0.001
-Robel (#; density)	5.048	0.277	3.983	0.215	1.124	0.254	4.43	0.007
Days 12+ Post-fledging								
Vegetation Density	0.181	0.116	-0.004	0.104	0.1832	0.076	2.42	0.250
-Average Height (cm)	65.800	3.165	60.689	2.951	5.084	2.255	2.25	0.266
-Total Cover (%)	76.156	2.154	76.711	1.986	-0.457	2.062	-0.22	0.861
-Concealment (%)	61.218	3.339	51.202	3.531	9.891	2.717	3.64	0.171
-Robel (#; density)	4.876	0.326	4.210	0.278	0.687	0.269	2.55	0.238

Fledgling Used vs Nest Locations								
Vegetation Characteristic	Fledgling Locations		Nest Locations		Mean Difference Fledgling – Nest	SE (Diff)	t	*P*
	Mean	SE	Mean	SE				
Days 0-3 Post-fledging								
Vegetation Density	-0.106	0.097	-0.013	0.092	-0.112	0.095	-1.18	0.272
-Average Height (cm)	57.856	2.413	55.816	2.424	1.547	2.596	0.60	0.568
-Total Cover (%)	73.020	2.085	77.010	1.927	-5.029	2.114	-2.38	0.045
-Concealment (%)	78.000	2.021	84.412	1.236	-6.566	2.805	-2.34	0.047
-Robel (#; density)	3.817	0.214	4.031	0.213	-0.270	0.221	-1.22	0.258
Days 4-11 Post-fledging								
Vegetation Density	0.336	0.094	-0.038	0.079	0.279	0.152	1.83	0.123
-Average Height (cm)	66.731	2.545	55.333	2.028	9.300	3.395	2.74	0.041
-Total Cover (%)	78.748	1.498	76.437	1.715	0.432	3.079	0.14	0.894
-Concealment (%)	79.210	1.741	84.099	1.246	-4.915	3.147	-1.56	0.179
-Robel (#; density)	5.048	0.277	3.989	0.187	0.906	0.410	2.21	0.078
Days 12+ Post-fledging								
Vegetation Density	0.181	0.116	-0.084	0.085	0.240	0.179	1.34	0.407
-Average Height (cm)	65.800	3.165	53.278	2.212	12.636	4.118	3.07	0.201
-Total Cover (%)	76.156	2.154	76.856	2.151	-0.228	4.270	-0.05	0.966
-Concealment (%)	61.218	3.339	85.684	1.334	-24.779	4.194	-5.91	0.107
-Robel (#; density)	4.876	0.326	3.831	0.193	0.885	0.442	2.00	0.295

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SUMMARY

My Master's Thesis focused on the post-fledging period—defined as the time between when a bird leaves its nest and disperses or migrates—of birds, a critical stage in the avian life cycle. Survival during the post-fledging period appears to be a key component in population growth and maintenance of bird species, therefore, understanding causes of variation in fledgling survival may be of critical importance in conserving avian biodiversity. I examined the post-fledging ecology of the Dickcissel (*Spiza americana*), with emphasis on pre- to post-fledging carryover effects of nestling traits and fledgling habitat use. From May to August of 2014 and 2015, I radio-tagged and monitored the survival of fledglings in two grassland locations of central Illinois, USA. While documenting fledgling survival, I also quantified vegetation characteristics of fledgling used, unused, and nest locations. Additionally, I used automated radio telemetry systems (ARTS) to document fledging activity rates continuously during the post-fledging period.

I found pre- to post-fledging carryover effects of body condition and wing development at fledging, in which traits were positively associated with survival during the early part of the post-fledging period. Survival benefits of each trait depended on cause-specific sources of mortality, such that individuals in better body condition were less likely to die from exposure while those with more advance wing development were less likely to be preyed upon. Fledglings in better condition and with more advance wing development were comparatively more active and mobile earlier in the post-fledging period, suggesting they were better able to evade and/or hide from predators. Fledglings used areas of greater vegetation density and areas with greater vegetation density were positively correlated with fledgling survival. The preferred habitat of

fledglings did not differ from nesting habitat. Collectively, my results add to a growing literature on the post-fledging ecology of birds, document several ways by which young songbirds mitigate the high risks of mortality during the early post-fledging period, and highlight important considerations for wildlife programs designed to conserve avian biodiversity.